Bee Pollination in Agricultural Ecosystems

EDITED BY

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FOREWORD

It was not until the eighteenth century that the subject of this book, the pollination services of bees, began to be understood and valued. Nevertheless, the association between man and bees has been long and close, and dates from at least 2400 BC. Beekeeping with the Western honey bee, *Apis mellifera,* was a well-developed craft in ancient Egypt during the fifth dynasty of the Old Kingdom. When Christopher Columbus and his companions landed in Cuba in 1492, the local inhabitants greeted them with gifts of honey from a local native stingless honey bee, *Melipona beecheii,* which was, and still is, managed in log hives by native peoples in the neotropics.

Man's close association with bees led to a remarkable cultural convergence between two of the great dynastic cultures: in ancient Egypt, the hieroglyph of a honey bee was a symbol of royalty, and for the Mayans of Central America a pictograph of a stingless bee was a symbol of kingship.

It is easy to see why this should be. On both sides of the Atlantic Ocean, honey and hive products such as wax and propolis from social bees were and are important commodities in human commerce, both as food and a source of cosmetic and medicinal substances. Together with fermented honey drinks, these honey bee and stingless bee products had immediate and obvious value and made it inevitable that apiculture would evolve into a respected craft that would often be accorded religious and magical status.

We can surmise, however, that an unwitting relationship with bees dates back even further. When our immediate ancestors embarked on the evolutionary path to bipedalism and a hunter-gatherer lifestyle, they could do so because of a savannah biotope with structural and floral features resulting from the coevolved interactions between those keystone mutualists *extraordinaire,* bees and flowering plants.

Now we are mostly *not* hunter-gatherers and we have produced new habitats, the agroecosystems, where intensive agriculture has resulted in crop yields undreamed of a couple of generations ago. In so doing, we have not emancipated ourselves from dependency on bees: we rely on them to pollinate 63 of the 82 (77%) most valuable crops. Worldwide, bees pollinate more than 400 crop species and in the United States more than 130 crop species.

This is not without some irony. While we still depend mightily on the pollination services of bees, we have devastated natural floras and insect faunas in creating vast, structurally uniform monocultures that are far from bee-friendly. Hence, the next stage in the evolution of man's close relationship with bees: the migratory beekeeper. In the ecological disaster zone known as California's Central Valley, vast numbers of honey bee colonies from as far away as Texas and Florida are trucked in each year for the pollination of almonds. In 1994 this involved the rental of 1.4 million honey bee colonies. By 2012, it is estimated that 2 million colonies will be needed for the ever-expanding acreage devoted to almonds alone. At the time of this writing, there are about 2.9 million honey bee colonies in North America, of which 2–2.5 million are rented out for pollinating 13 crops.

The arithmetic of future needs, therefore, doesn't quite add up. This, together with the fact that honey bees are under growing pressure from parasites, disease, and colony collapse disorder, has understandably led to the search for additional native bee species as alternatives to honey bees as managed pollinators.

It is to the wildlands and their floras that we must look for new pollinator species, and this is happening. However, we must conserve these reservoirs, many of which are under pressure from urban sprawl and agriculture. To do this, we need to develop a greater understanding at the community level of the dynamic network of relationships between bees and flowering plants. This is not simply for the economic benefits of potential pollinators: we also accord aesthetic and recreational value to our wildlands.

Research on the nesting biology and management of native, solitary bees for specific crops is now a growing field. Moreover, we can enhance our use of the pollination services of these bees by attempting to overcome corporate agriculture's horror at the prospect of stands of native flora as supplementary forage in the vicinity of their crops.

Biosecurity can be regarded as a recurrent theme in this book, whether it is concern about pollen transfer from genetically modified crops to related weed species, mediated by the foraging movements of bees, or the unforeseen and detrimental interactions between invasive plants and native bee faunas. Unforeseen and adverse ecological effects also occur when bee species and/or subspecies are moved outside of their natural ranges. The best known example of this is the problem of "Africanized" honey bees, when bees from sub-Saharan Africa were introduced into Brazil, crossed with European honey bees (also nonnative), resulting in a multiplicity of well-known problems. Problems also have occurred with the commercial management of bumble bees for greenhouse crops, where subspecies of *Bombus terrestris* have been introduced outside of their natural range, and now cases in England and Israel document the escape and establishment of populations into the wild, with adverse effects on local bee faunas.

The above issues are outlined and discussed in this book. These are pressing matters, and this volume is therefore timely, not least because its contributors are leading current thinkers and researchers in the field. Collectively, the subjects they address indicate the broad front of future research that is necessary if we are to consolidate our relationship with bees and their sustainable exploitation and management.

The agenda is therefore set, and we will succeed. We have to. Otherwise, under “any other business,” ecologically-minded people of my generation might well ask, “How will my grandchildren cope with the food riots?”

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Part 1

Bee-Provided Delivery Services

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1 Bees in Nature and on the Farm

Theresa L. Pitts-Singer and Rosalind R. James

Introduction

When we say that we work at "the Bee Lab," most people automatically imagine us decked out in bee suits, standing next to box-shaped hives, and holding our breaths amidst a barrage of honey bees. Although our research facility is one of five U.S. Department of Agriculture's Agricultural Research Service laboratories that are dedicated to bee research, our focus is unique in its emphasis on non-honey bees that are important or potential pollinators. The other four U.S. bee research facilities focus on honey bees, examining various aspects of honey bee biology, pest control, management, and pollination. As we have grown in our understanding of the importance of a variety of bees as pollinators in agricultural systems, we have been inspired to compile this book.

This book illustrates the importance of both managed and wild bees in agricultural ecosystems. For much of agriculture, the vital role that pollinators play in successful crop or seed production is clear and direct. Commercially managed bees are available for pollination services and are used in large commercial fields, small gardens, or enclosures such as greenhouses and screen houses. Although the general public gives honey bees much of the pollination credit, managed bumble bees and solitary bees also have made a great impact on certain commodities, and wild bees provide free pollination services that often go unnoticed. However, all of these bees are valuable and significant in their liberal passing of pollen from one plant to the next. With the recent concern over the unexplained loss of honey bee colonies, referred to as colony collapse disorder, it seems ever more important to highlight some of the other bees that could be managed for crop pollination.

Just how important are wild and managed bees in the agricultural ecosystem for the successful production of seeds, fruits, and vegetables? What is the contribution of bees to maximizing crop production and what is the effect of human manipulation and control on both the bees and the plants they visit? Do we know how to use managed bees in the most effective, sustainable, and profitable manner? Are novel uses of managed bees awaiting discovery or implementation? What is the interplay of wild and managed bee populations in natural and commercial settings? Revealing answers to such questions and posing new questions in light of these answers are goals of this book.

Crop pollination by bees and other insects in temperate and tropical agricultural systems has been reviewed extensively in several informative books. These books often are organized according to crop type or plant family or according to pollinator species and their use for seed or fruit production. However, these books do not present a comprehensive look at the ecology of bees in agricultural systems. Certain environmental factors have a substantial impact on bee pollination ability and survival rates; conversely, the bees can affect the ecosystem through their foraging activity, their interactions with plants and other pollinators, and their invasiveness in novel localities. We invited bee researchers and pollination biologists with various areas of expertise to highlight ecosystem-level approaches to and conceptions of the study of bees in agriculture. Some authors highlight the overall efficiency and effect of managed and wild bee activity in fields and greenhouses or the novel use of bees for nonpollination functions such as the spread of microbial pest control agents. Other authors address the details and difficulties of managing solitary bees for alfalfa seed and tree fruit production, as well as the development of new pollinators for nonfood seed crops. Considering environmental risks, the final chapters are dedicated to an ecological awareness of bees beyond crop production, such as the impact of exotic bee introductions on other pollinators and plants, the interactions of bees with invasive plant species, and how bees mediate gene flow within and outside of fields of hybrid or genetically engineered crops.

We intentionally have omitted some topics related to bees in agricultural systems. We decided not to include a chapter dedicated to honey bees because honey bee management is covered thoroughly in many other publications. Instead, we cover honey bees as they relate to the various topics of discussion throughout the book. We also do not include much discussion of the stingless bees in the tropics, mainly because these bees are primarily utilized for a very small, specialized honey market and it is still unclear whether attempts will be made to use them on a broader agricultural scale. Exactly how these bees will be used and the extent of their use has not yet been demonstrated.

Definition of a Bee

What exactly is a bee, and why are bees so important for pollination? Bee pollination is best understood if one can first distinguish bees from each other and from other related insects and if we know their evolutionary and natural history. Bees, wasps, and ants are in the insect order Hymenoptera. Genetically, the sex of all hymenopteran insects is determined through the mechanism of haplodiploidy. For the bees, this means that males have only one set of chromosomes (i.e., are haploid) and females have a pair of chromosomes (i.e., are diploid). This can occur because male bees are produced from unfertilized eggs and females develop from fertilized eggs. An egg-laying female can control which eggs get fertilized and which do not, and in this way, she is able to control the sex ratio of her offspring. The sex ratio of the pollinator population is important because female bees pollinate many more plants than males do. The main purpose of females visiting plants is to collect enough pollen and nectar to feed their young. Males, on the other hand, need to visit only enough plants to feed themselves (they visit no flowers if they are fed by the females, as occurs with honey bee and bumble bee drones).

Bees and sphecid wasps belong to the superfamily Apoidea. The bees (called Apiformes) can be distinguished from the wasps by the presence of erect, plumose hair on their faces (Michener, 2000). Bees are very diverse and abundant, with more than 16,000 species worldwide (Michener, 2000). Yet the true number of bee species is basically unknown, because not all have been given a name, and some have yet to be recognized or discovered. Different sources give different answers about the exact diversity of bees, and the variation in answers depends on what species were known at the time of the publication and how the bees were classified. For example, for the region of North and Central America, one finds reports of between 77 and 165 bee genera, represented by between 2,600 and 4,900 species (e.g., Krombein et al., 1979; Michener et al., 1994; Michener, 2000).

Unlike the predaceous wasps, bees are pollen collectors (with the exception of the highly derived stingless bees, *Trigona* spp., that eat carrion). Bees probably came into existence around 120 million years ago during the mid-Cretaceous, prior to the radiation of angiosperms (Grimaldi & Engel, 2005). Because most modern bees are dependent on the products of angiosperm flowers—including pollen, nectar, and oils—the evolutionary overlap of bees and angiosperms is not surprising. The coevolution of bees and flowers has resulted in special morphological adaptations for both insects and plants, and the need of some plants for pollination by bees is absolute.

Over evolutionary time, some bees developed preferential relationships with only one or a few plants (oligolecty), but others maintained a more general preference for a wide range of flowering plants (polylecty). And conversely, for some plants, only one or a few bees are able to provide pollination with the proper behavior or morphology, and these bees are often attracted to the plant by its unique fragrance or appearance (Barth, 1991; Proctor et al., 1996). In at least one case, a plant, the death camus, produces a toxin to protect itself from herbivores, and few bee species are uniquely adapted to ingest and thrive on the plant's toxic pollen (e.g., Tepedino, 2003). But pollen is not the only plant product affected by coevolution. Nectar is located in specialized flower parts called nectaries, and sometimes the morphology of the flower creates exclusive access to this resource by requiring an insect to exhibit a particular behavior or to have appropriate morphology (e.g., bee tongue length or body size; Barth, 1991; Free, 1993; Proctor et al. 1996).

Bees have also evolved a variety of social systems. The bees commonly used for pollination fall into the categories of highly eusocial, primitively eusocial, and solitary. Eusocial insects include all ants, some wasps and bees, and termites. Eusocial hymenoptera are defined by three criteria: (1) only one or a few females in a colony reproduce; (2) the colony consists of individuals from overlapping generations, including one or more queens plus her daughters and sons; and (3) brood care is cooperative within the colony. No single theory alone suffices to explain how eusociality evolved or how it is maintained. It has been theorized that altruistic, cooperative behavior can be explained by a close relatedness among cooperating individuals, but such a theory does not fully explain the social complexity of insects that live in colonies, because not all social insect societies are composed of close relatives. Reproduction and cooperation in the colony is usually controlled by the queen. For the highly eusocial honey bees, the queen maintains reproductive dominance over the workers by producing a chemical compound called queen pheromone. In the primitively eusocial bumble bees, queen pheromonal control is not well developed, and aggressive behavior toward other egg layers is the prevailing enforcement strategy (Michener, 1974).

In honey bees, the female queen and workers are strikingly different in behavior, physiology, and morphology. The queen honey bee would die if left without workers because she is designed only for mating and reproducing, not for foraging and brood care. Honey bee colonies also are long-lived and store food for colony members to use during times of dearth or inclement weather and during the winter. Primitively eusocial bumble bee queens are structurally equivalent to workers but are larger in size. Unlike honey bees, bumble bee queens live alone at the beginning of the colony cycle, foraging and taking care of the brood until the first workers emerge. Bumble bees store small amounts of honey and pollen for adults and brood, but the colony is usually short-lived and does not persist through the winter (Michener, 1974; Heinrich, 1979). Only the new generation of reproductive females, already mated, hibernates over the winter period. However, colonies of the European bumble bee *Bombus terrestris* have persisted throughout the recently milder winter months in England and New Zealand, which may demonstrate phenological plasticity in this bee species (Goulson, 2003). Other primitively eusocial bees include many sweat bees (Halictinae) and carpenter bees (Xylocopinae; Michener, 1974).

In many respects, each female solitary bee is both a “queen” and a “worker” at the same time. Solitary bees do not form colonies and have no social colony structure. A solitary female constructs her own nest and then provides food for each of her brood in the form of a mass of pollen and nectar. After this, she usually dies or departs without further care to her young and before her offspring complete their development. As a result, there is no chance for cooperation between mothers and daughters. The adult life of these bees is short, spanning only a matter of weeks. Solitary bees may nest alone, or they may nest in aggregations. Commonly, nest aggregations occur among bees that nest in the soil, but some cavity-nesting bees will form aggregations if nesting sites are available, as is common with alkali bees, mason bees, and leafcutting bees (Michener, 1974). The tendency for some solitary bees to form nest aggregations makes them particularly amenable to management for agriculture because it allows farmers to provide concentrated nest sites for the bees.

An Industrious Hum

Why are bees such notoriously hard-working pollinators? Bees are the ultimate pollinators. They are superior to other flower-visiting insects in pollination efficacy for many crops because of their abundant pollen-trapping body hair, specialized flower-handling and foraging behaviors, and reliance on floral rewards for raising offspring (Free, 1993). What benefits are gained from plants by the bees? For bees, it is all about collecting pollen and nectar and, in some cases, essential oils. These rewards are produced by plants and collected by bees as food for their brood and as fuel for adult activities. What benefits are gained from bees by the plants? For flowering plants, it is all about improving reproduction and spreading their genes. The plants benefit when bees come into contact with the reproductive structures of flowers. Bee activity increases pollen movement because the bees transport pollen grains from flower to flower and from plant to plant, delivering them to receptive stigmas and providing for cross-pollination.

Most people think of pollen as a larval bee food that is high in protein. Indeed, pollen contains 16–60% protein, but also can be a source of fats, starches, sugar, phosphates, vitamins, and sterols (Standifer et al., 1968; Svoboda et al., 1983; Buchmann, 1986; Barth, 1991; Proctor et al., 1996). Most flowers offer both pollen and nectar, but some offer only pollen. Millions of pollen grains are available per flower for a bee to collect, and such an abundance of pollen grains creates an ample resource of genetic material for plant propagation, in addition to being a source food for the propagation of plant pollinators (Barth, 1991; Proctor et al., 1996).

Nectar is commonly thought of as a carbohydrate reward offered to pollinators. Sugar (15–75%) and water are the main nectar ingredients, but other nutrients are also present, including amino acids, proteins, organic acids, phosphates, vitamins, and enzymes. Unlike pollen, nectar is not transferred between flowers by bees and plays no direct role in a plant's reproduction. However, because nectar attracts insects to flowers and is a vital component of larval provisions, nectar indirectly promotes pollination. Some plants produce oils as floral rewards that are collected by bees. Oil-collecting species include solitary bees in the families Andrenidae, Anthophoridae, and Mellitidae, and also the orchid bees (Apidae: Apinae: Euglossini). Depending on the species, these bees collect oils to mix with pollen (and may also add nectar) as a rich, fatty food source for larvae. Some bees may use oils in making water-resistant cell linings. Male euglossine bees collect highly scented flower oils from various orchids and use them to facilitate their own attractiveness to mates (Proctor et al., 1996; Roubik & Halson, 2004), and while collecting oils, these males serve as pollinators.

Consideration of Bees' Needs

For maximized production of many crops, bee pollination is required as part of a complete management system. The most successful pollination will occur when crop managers implement strategies that consider the needs of the bees. In most agricultural systems that require insect pollination, bees cannot be treated like a field application of fertilizer or herbicide. Whether managed or naturally occurring, bees need food and safe harbor for living and reproducing. If the needs of bees are met, then thriving pollinator populations will be available to provide their services year after year.

For managed bees, the timing of bee release onto a crop must co-occur with bloom so that resources are available for the bees and so that timely pollination occurs. If the crop is not in bloom when bees are ready for release, other flowering plants could be provided to maintain bees until the onset of crop bloom, or other strategies need to be taken. For example, managed solitary bees can be chilled for a short period to delay their development and facilitate timing their emergence with bloom. Failure to provide a floral resource for active bees decreases the reproductive success of bees and, in some cases, may cause them to leave the crop vicinity in search of alternative forage. Additionally, providing adequate and desirable nesting places will promote better bee retention and reproduction. Inundating a crop with pollinators may guarantee maximum crop pollination, but using an alternative method—a lower, sustainable number of foraging bees—may reduce competition for food and nesting resources, bringing about both high crop yield and greater bee reproduction rates.

Managing bees can be problematic due to the dynamics of rearing organisms in close proximity and in controlled situations. Disease epidemics can devastate or impair the production of commercial pollinators, and research is ongoing on bees that have been used domestically for thousands of years (such as the honey bee), on bees managed for decades (such as alfalfa leafcutting bees and bumble bees), and on bees on the brink of commercial-scale use (such as the red mason bee and the blue orchard bee).

In addition to managed bees, it is important to recognize the potential benefits of wild, native bees in crop systems. Mark Winston offers an encompassing view of how managerial practices might discourage wild bee pollination: "The reason that wild bees no longer visit crops are few and clear: pesticides, lack of floral diversity, habitat destruction, and, ironically, competition with managed pollinators" (Winston, 1997, 119–120).

Although wild bees are not managed, especially not in the same way as commercial bees, certain practices on or near the farm can encourage their availability and likelihood of flower visitation. If native bees already are performing a pollination service in a crop system, the addition of managed pollinators may cause competition for food and nest sites, which could result in reduction or elimination of natural pollination. Wild bumble bees, carpenter bees, sweat bees, mason bees, and other bees will visit crop flowers if favorable habitats occur in the vicinity. Favorable habitats are those in which food and safe nest sites can be found. Whether naturally or artificially created, bare patches of undisturbed ground or persistent embankments may increase aggregations of ground-nesting bees, such as alkali bees and sweat bees. Old wooden structures, loose debris piles, and thick underbrush may be attractive to carpenter bees and bumble bees as nest sites. Old, pithy plant stems, hollow reeds, or boards with drilled holes may be inviting to cavity-nesting leafcutting and mason bees. Naturally occurring flowers or deliberately added flowering plants may provide alternative sources for pollen and nectar to keep bees in a production area before the onset of crop bloom or after it has passed.

Thus, when the more preferred crop flowers are available, the bees will be available to pollinate; when the crop flowers disappear, the bees can complete their nesting.

Conclusion

Bees are extremely vital to the well-being of mankind. Products from pollinated plants, including fruits, vegetables, and seed crops, not only feed people but also feed the pets and livestock that people raise for pleasure and consumption. An appreciation of the vital relationships between plants and their pollinators, in their own time and space, is needed to secure the future of crop production. The chapters in this book are intended to provide valuable information and forethought for understanding the impact of bees in the dynamic agricultural ecosystem of modern society.

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2 Crop Pollination Services From Wild Bees

Claire Kremen

Introduction

Historically, crop pollination needs were met by wild pollinators living within the farming landscape (Kevan & Phillips, 2001), and this is still true in less intensive agricultural systems (e.g., Ricketts et al., 2004; Morandin & Winston, 2005). For many modern crops requiring an animal pollinator, however, pollination is now managed as intensively as other aspects of agriculture by bringing large numbers of commercial pollinators directly to the field where pollination is needed.

Only a dozen species have been commercialized for use as pollinators (Parker et al., 1987; Batra, 2001), although thousands more species, primarily bees, participate in crop pollination (Nabhan & Buchmann, 1997). The most widely used pollinator, and the one with the longest history of domestication, is the honey bee, *Apis mellifera* (Crane, 1990), probably utilized for at least 90% of managed pollination services (Calderone, personal communication, 2005). The extent of our reliance on this single species for such an important service is risky. In the United States, managed stocks of the honey bee have declined by 50% over the past 50 years (National Research Council, 2007) due primarily to the mite, *Varroa destructor* (Morse & Goncalves, 1979; Beetsma, 1994), which both weakens individuals and transmits disease. Also, *Varroa* mites have developed resistance to the miticides (Elzen & Hardee, 2003), leading to high rates of over-winter colony mortality during some years (e.g., up to 50% across large areas of the United States), and thus high within- and between-year variability in the honey bee supply (National Research Council, 2007). *Varroa* has affected honey bee availability not only in the United States but also in Europe and the Middle East (Griffiths, 1986; Komeili, 1988).